Trends in Plant Science

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Opinion

A Wood Biology Agenda to Support Global Vegetation Modelling

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Realistic forecasting of forest responses to climate change critically depends on key advancements in global vegetation modelling. Compared with traditional 'big-leaf' models that simulate forest stands, 'next-generation' vegetation models aim to track carbon-, light-, water-, and nutrient-limited growth of individual trees. Wood biology can play an important role in delivering the required knowledge at tissue-to-individual levels, at minute-to-century scales and for model parameterization and benchmarking. We propose a wood biology research agenda that contributes to filling six knowledge gaps: sink versus source limitation, drivers of intra-annual growth, drought impacts, functional wood traits, dynamic biomass allocation, and nutrient cycling. Executing this agenda will expedite model development and increase the ability of models to forecast global change impact on forest dynamics.

Highlights

'Next-generation' global vegetation models track the performance of individual trees as a function of light, carbon, water, and nutrient availability, explicitly include forest demography, and simulate disturbances. This model development involves a major increase in complexity and in the amount of simulated processes.

The development and quality of next-generation models critically depends on the availability of insights to simulate these additional processes. Yet, knowledge on key processes such as sub-annual tree growth, source- versus sink-limited growth, dynamic biomass allocation, drought effects, and nutrient cycling is currently poorly available.

Wood biology can importantly contribute to filling this knowledge gap by providing knowledge on crucial processes for tree functioning. This field of science is well positioned due to recent progress in concepts, measuring tools, and analyses.

From One Big Leaf to Many Trees

Forests play a crucial role in the global carbon cycle and climate system [1]. Forest responses to climate change have direct implications for regional climate, carbon uptake, biodiversity, and society. Sound predictions of forest responses to climate change are therefore crucial. Since the 1990s, **dynamic global vegetation models (DGVMs)** (see Glossary) have been used to forecast forest responses to climate change and forest-climate feedbacks [2]. First-generation DGVMs treated forest canopies as a 'big leaf', simulated forest productivity as a function of leaf photosynthesis, and simplified forest demography as 'area-based' birth and death [3]. Recent advances have produced DGVMs that include nutrient cycling, account for limitations of water uptake and transport, allow more (characteristic) **plant functional types**, track the growth of tree individuals and cohorts, and describe detailed forest demographics [4–7] (Box 1). Ongoing development will lead to next-generation models that simulate carbon-, water-, and nutrient-limited dynamics of tree organs and trees, and scale up to forest dynamics through processes of competition, recruitment, and disturbance. Such model development requires insights into a wider array of processes, at a larger range of temporal and spatial scales, and for a larger number of species and/or functional plant types. Insufficient data and patchy insights may seriously limit the quality and application of next-generation models; an issue that has so far received scant attention.

In this opinion article, we argue that **wood biology** can provide essential contributions to developing next-generation models. We first briefly review required knowledge for these models and then outline a wood biology research agenda to support model development, parameterization, and validation. We consider wood biology to include **dendrochronology**, **dendrochemistry**, **wood anatomy**, wood-based physiology, **dendrometer** studies, **xylogenesis** studies, and sap flow studies.

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Box 1. Dynamic Global Vegetation Models: A Brief History

Terrestrial DGVMs were originally developed to provide insights into the transient responses of vegetation to climate variation and disturbance [2], and to estimate biospheric exchanges of carbon, water, and energy. Nowadays their applications are extending to evaluating ecosystem services and climate mitigation strategies [84]. Current-generation DGVMs aim to overcome several key problems that have hindered 'big-leaf' models, including improved radiative transfer (sun versus shade leaves), diffuse versus direct radiation, more realistic demography by representing individuals, and new approaches to focus on dynamic rather than fixed traits. These models include an explicit representation of tree size and stand age. While such size- and age-structured modelling frameworks were developed at the same time as first-generation models [85,86], theoretical and computational challenges initially prevented their adoption in Earth system models. The size- and age-structured framework allows for direct comparison of variables measured in the field. For example, cuvette measurements of photosynthesis along leaf nitrogen or radiation gradients can be linked directly to the modelled conditions, and results of demographic field studies can be directly compared with model output.

Following the calculation of net primary production, most DGVMs allocate carbon to a sequence of biomass pools that include sapwood, roots, foliage, nonstructural carbohydrates, and reproductive organs [87]. Early allocation schemes were based on resource-limitation approaches [88], in which net primary production, or 'biomass increment', was allocated to biomass pools most limiting to productivity (e.g., roots under water limitation; leaves under light limitation). These schemes generally overlooked functional constraints such as sapwood supporting leaf area [89] and leaf-to-root ratios. Allocation schemes in current-generation models rely on simultaneously satisfying both allometric and functional constraints. Evolutionarily guiding principles (evolutionarily stable states, metabolic scaling) are emerging as techniques to balance these constraints [90–92].

Tree growth and carbon allocation are tightly linked to nutrient availability but this is often overlooked in models [93]. Next-generation DGVMs include interactive representation of the main macronutrients: nitrogen and phosphorous. Nutrient uptake is modelled as either a passive (concentration-based) process [94] or as an active (demand-based) process [95], and within-organ allocation of nutrients controlled by stoichiometric constraints and priorities of nutrient use in leaves, enzymes, and cellular maintenance. Large process and data uncertainties have slowed the pace of developing nutrient-limited DGVMs, but progress in individual to cohort-based models, multilayer canopy structure, and differentiation of sun and shade leaves allows better integration of field measurements in models.

Hungry Models

Next-generation DGVMs aim to accurately simulate carbon, nutrient, and water cycling in forests by scaling from tissue, through tree organ, individual tree, population, stand, and landscape to the grid cell (Box 1, Figure 1). At tissue, organ, and individual tree levels, the availability and fluxes of water, light and thermal energy, nutrients, and carbon co-determine rates of biomass growth and loss. These processes are driven by, and feedback upon, a number of environmental variables, and moreover depend on genotypic and phenotypic characteristics of tree species or plant functional types. At stand level, demographic processes and competition determine biomass loss and gain. Stand dynamics are forced by natural (e.g., fire, flooding, wind throws, insects) or human disturbances and management. At landscape or grid cell levels, the scales at which DGVMs are coupled with Earth system models, atmospheric CO_2 exchange is calculated from net biomass gains and losses, water relations are derived from total evapotranspiration, and vegetation albedo and surface roughness, determine energy relations.

Current- and next-generation DGVMs struggle to faithfully include all processes shown in Figure 1, due to theoretical and computational challenges as well as data limitations. We will not list required parameters for models, but limit our review to broadly evaluate the availability of insights and data on processes included in Figure 1. Detailed descriptions of data requirements are found in publications of current-generation DGVMs that include nutrient limitation [5,8], tree demography [9,10], advanced plant hydraulics [11], turgor-driven growth [12], temperature-limited growth [13], **source limitation** or **sink limitation** [14], functional traits [15], competition [16], and fire effects [17]. Based on these lists and our judgement of data availability, we highlight processes in Figure 1 that are poorly understood or quantified. These mostly relate to growth of cells and tree organs, nutrient and water cycling in individual trees, and below-ground processes at stand level.

Glossary

Benchmarking: a procedure comparing model output with independent empirical observations of processes, structure, or development (of vegetation).
Big-leaf models: a class of DGVMs that simulates carbon, energy, and water fluxes of vegetation canopies based on a characteristic leaf in the top of canopy.
Climate-growth analysis: the study that relates temporal variation in tree growth (from a chronology) to that in climatic variables.
Dendrochemistry: the field that studies chemical composition and chemical processes in wood. This includes measurements of stable isotopes ratios, nutrients, trace elements, and organic components.
Dendrochronology: the field that studies time series of tree-ring width (or other measurements) of individual trees to produce a time series of common deviations of these measurements within a population: the 'chronology'.
Dendrometer: a device that measures temporal variation (at minute to month scale) in stem circumference (band dendrometer) or stem diameter (point dendrometer) caused by stem water uptake, stem drying, structural phloem and xylem growth, and collapse of phloem cells.
Dynamic Global Vegetation Models (DGVMs): a class of simulation models that predicts the development of terrestrial vegetation (and climate-vegetation feedbacks) under projected future climate and land use.
Forcing variables: environmental conditions and (human-induced) disturbances that influence tree growth and forest dynamics in DGVMs.
Hydraulic failure: the situation in which trees cannot move sufficient water from roots to leaves because a drought-induced loss of water transport capacity.
Nonstructural carbohydrates: all carbohydrates produced by photosynthesis that are not embedded in structural tissue of plants, such as cell walls and fibers.
Plant functional type: groups of plant species in DGVMs with similar photosynthetic pathways, phenology, growth form, or functional traits.

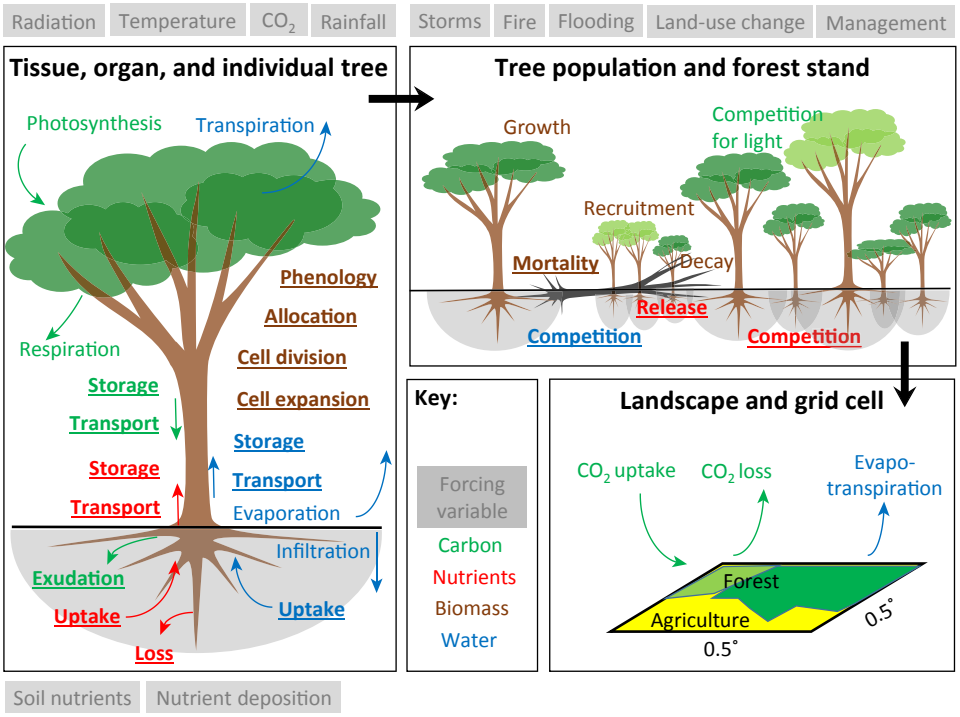

Figure 1. Simulated Processes in Next-Generation Vegetation Models. Processes are organized in three broad levels (panels), grouped by type (color), and highlighted (bold and underlined) when poorly understood or quantified. To reduce space, many nutrient fluxes (mineralization, deposition, leaching) and all energy fluxes are left out.

How Wood Biology Can Contribute

Wood biology is well positioned to fill major data and knowledge gaps for next-generation models (Box 2, Figure 2). Wood biological studies deliver insights into individual tree performance [18] (the simulation unit of these models) and do so at the high temporal resolution at which trees respond to climatic variation (and extremes) and models simulate processes [19,20]. Wood biological studies are supremely flexible to yield insights for nearly any choice of forest type, location, tree species, and process resolution from cellular and sub-daily scales to continental and centennial scales. Whereas finer spatiotemporal scales routinely yield insights into mechanisms and processes, long-term wood biological studies using tree-ring analyses allow model **benchmarking** at decadal to centennial time-scales, relevant for model validation and policy decisions [21,22].

These foreseen contributions of wood biology to model development complement those of other disciplines. For instance, remote sensing has been important to evaluate model output on forest canopies and leaf phenology [23] in near real-time and at global scales. Yet, optical satellite instruments cannot reliably monitor forest biomass productivity [24]. Eddy flux measurements have been instrumental in calibrating simulated stand-level gross primary productivity (GPP) [25], but do not provide direct information for individual trees or sub-tree level processes. Plot-based monitoring of forest dynamics are crucial to calibrate, initialize, and benchmark models by delivering rates of tree growth, mortality, and recruitment, and estimates of stem density, forest biomass, tree allometry, and biomass trends [26,27]. International plot networks

Sap flow sensor: a device consisting of two to four metal pins (inserted in functional tree sapwood) that estimates xylem water flow by generating heat (pulses) and measuring heat movement in sapwood.
Sink limitation: the situation in which plant biomass growth is limited by the ability of (leaf, wood, stem) tissue to grow (cell division, cell enlargement, and cell wall thickening), due to insufficient availability of water or nutrients, or unfavorable thermal conditions.
Source limitation: the situation in which plant growth is limited by the availability of carbohydrates produced by photosynthesis due to low radiation, low atmospheric CO_2 pressure, or stomatal closure.
Water use efficiency: a measure of the amount of photosynthesis realized by a plant per unit of water lost through transpiration.
Wood anatomy: the study that describes and quantifies the structure of different components of wood.
Wood biology: the discipline that studies processes taking place in tree (or shrub) stems or derives insights on tree functioning from studying wood characteristics. This includes dendrochronology, dendrochemistry, wood anatomy, wood-based physiology, dendrometer studies, xylogenesis studies, and sap flow studies.
Xylem vulnerability curve: the result of measuring water transport capacity of wood tissue at different water potentials (or temperatures), yielding insights into tolerance to drought (or frost).
Xylogenesis: the process of formation of wood tissue, including the timing and rate of xylem cell division, cell expansion, and cell wall thickening.

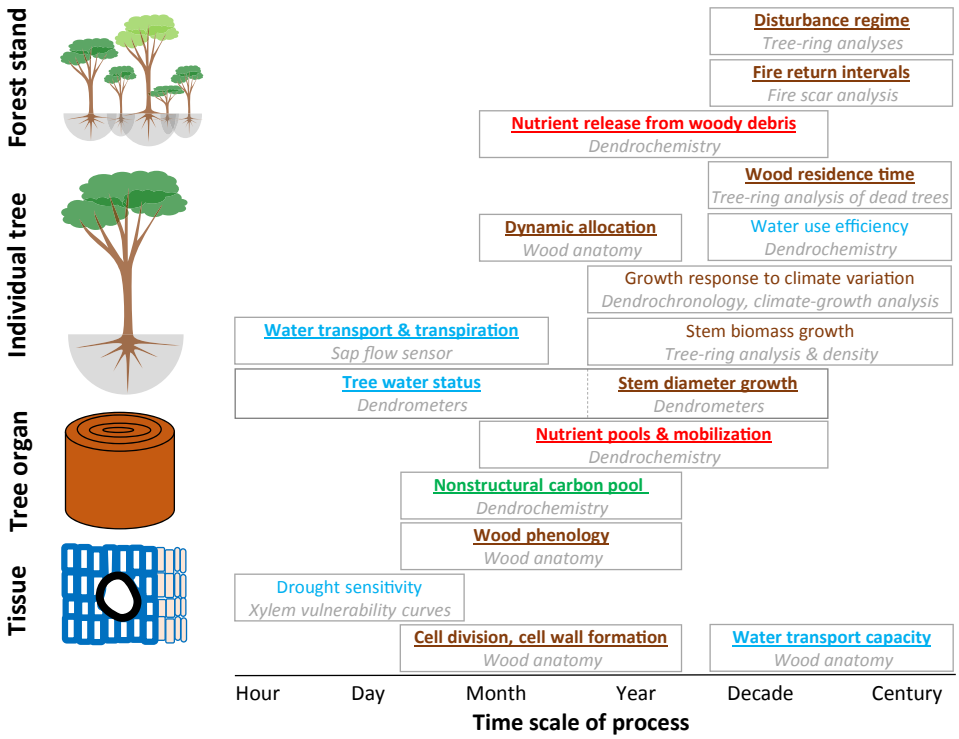

Figure 2. Contributions of Wood Biology to Next-Generation Vegetation Models. Shown are simulated processes at different organizational levels that can be quantified by wood biological studies (methods in *italic*). Processes are grouped by type (color) and are highlighted (bold and underlined) when poorly quantified or understood. The dashed line between 'Tree water status' and 'Stem diameter growth' illustrates the difficulty in separating structural growth from fluctuations in stem water content in dendrometer measurements.

provide additional virtues towards benchmarking across climatic gradients and forest types [28,29]. Yet, plot studies rarely yield information at the level of individual trees and are carried out at coarse temporal frequencies (i.e., every 5 years). Finally, large-scale ecosystem manipulation experiments (CO_2 enrichment, warming, rainfall exclusion, nutrient addition) are excellent frameworks for model benchmarking [25,30] and can assist in model development [31]. However, the scale, replication, and representativeness of such experiments is necessarily limited by their high costs. Complementary wood biology investigations can help overcome some shortcomings of the above methods.

A Wood Biology Research Agenda

Our proposed research agenda is structured according to six interconnected knowledge gaps. To fill these gaps, we propose specific wood biological studies (Figure 2) and explicit collaboration with other disciplines, in particular for gaps 5 and 6.

1. Understand wood formation within the year.

Dendrochronologists have a reasonably good understanding about the climatic drivers of annual stem growth. **Climate-growth analyses** of tree-ring data have revealed the important roles of rainfall, temperature, and drought in determining annual stem growth [21,32]. While

Box 2. Recent Conceptual and Methodological Advances in Wood Biology

Recent progress in wood biology is now leading to paradigm shifts in the understanding of wood functioning, tree growth, terrestrial vegetation status, and dynamics. These advances can be framed in the context of a remarkable expansion of both the spatial and temporal scale of measurements. At the fine spatial and temporal scales, progress in understanding annual growth in stem volume and biomass is based upon observations of cell growth and stem dynamics, and how these are driven by climate, phenology, and hormonal regulation [20]. Moreover, the development of automated point dendrometers, **sap flow sensor**, and water potential sensors allows continuous, high-frequency measurements of tree hydraulics and structural stem growth at scales of minutes to years [19,96]. Advances in field investigations are complemented by parallel progress in quantitative wood anatomy, especially with the development of 3D wood scanning tools [97] and software for rapid and precise analysis and interpretation of 2D scans [98–100]. These fine-scale investigations are contributing to a process-based understanding of plant response to environmental variation, an endeavor crucial to bridging the physiological and global change scales. Towards the other end of the spatial and temporal expansion, data streams are becoming available for an increasing number of sites, forest types, and species, at time scales of years to centuries. Ongoing efforts to standardize dendrometer and tree-ring data [101], publish statistical analysis tools in publically available packages [75,102,103], manage worldwide tree-ring networks [79], derive regional tree growth anomalies from tree-ring data [105], and setup networks for dendrometer and sap flow measurements [52,104] will provide highly valuable data sources for model benchmarking (Figure 2). The recent advances in wood biology allow understanding and measuring processes at fine temporal resolution and thus contribute to breaking conventional scales for data and analyses in vegetation modelling. The tree ring, calendar year, and individual tree no longer need to be the default measurement unit, but may partially be replaced by the wood cell, day (or month), and tree organ.

these climate-growth relations offer valuable information for model benchmarking, their annual scale does not match the time steps at which next-generation DGVMs operate. Model development requires insights on environmental and hormonal control of wood formation within the year (xylogenesis [33]), but such knowledge is scantly available. Insights are required on two distinct processes: stem volume growth, which is driven by processes of division and enlargement of xylem and phloem cells (including vessels), and stem biomass growth, which is chiefly driven by cell wall formation and the density and sizes of cells [20,34,35]. Including these insights into next-generation models may require a paradigm shift from simulating stem diameter or biomass growth, to simulating wood cell development. Information on the seasonal rhythm of wood growth ('wood phenology') offers additional options for model benchmarking [36], as patterns and drivers of wood phenology differ from those of leaf phenology [37,38]. Wood formation and phenology can be directly studied via xylogenesis monitoring [20] or cautiously inferred from dendrometer measurements [39].

2. Quantify relative strength of sink and source limitation of tree biomass growth.

A fundamental challenge in vegetation modelling is to mechanistically address both source and sink limitations of tree growth. Specifically, the extent to which tree growth is limited by the availability of sugars produced by photosynthesis (source limitation) versus the conditions that allow cells (in leaves, roots, wood, bark) to enlarge and divide (sink limitation), is poorly understood [12,40,41]. If growth is mainly source limited, increasing atmospheric CO_2 concentration may strongly fertilize tree growth. In contrast, when tissue formation is sink limited, tree biomass growth may be less responsive to CO_2 rise. While forest productivity in 'big-leaf' models assumes a first-order source limitation, and may yield potentially unrealistic CO_2 fertilization rates [42], next-generation models should simultaneously and fundamentally consider both source and sink limitation (due to nutrient limitation [5], water shortage [11], and turgor-driven [12,43] and temperature-limited growth [12]). Inferences on sink versus source limitation can potentially be estimated in dendrometer studies in which sap flux and turgor pressure are also recorded [19] and in studies combining tree-ring, xylogenesis, and photosynthesis measurements with mechanistic tree growth modelling [44].

3. Quantify the mechanisms and implications of drought impacts.

Many forests will experience increasing drought frequency and intensity under climate change, due to warming and reduced water availability. Droughts strongly influence tree growth and mortality [45], by limiting carbon availability, decreasing cell turgor, and/or causing **hydraulic failure** [46]. **Big-leaf models** allow droughts to affect trees only through carbon starvation. Next-generation models should consider how drought reduces tree growth and survival through hydraulic failure for trees of different size. There is now evidence from field studies that drought-induced hydraulic failure enhances tree mortality [47–49], and from modelling studies that simulated tree mortality matches observed values more closely when hydraulic failure is included in DGVMs [50]. Impacts of warming and reduced water availability can be partially compensated by stomatal responses to atmospheric CO_2 rise, which reduces tree water loss and increases **water use efficiency** [22,51]. Wood biological studies can provide important contributions to quantifying and understanding drought impacts on tree growth, mortality. and water relations. Possibilities include: relating **xylem vulnerability curves** to drought-induced mortality or growth declines [48]; measurements of stem dynamics, sap flow, and xylogenesis during droughts [52] or in manipulation experiments [47,53]; stable isotope studies to infer water use efficiency changes driven by increased atmospheric CO_2 rise [22,51]; tree-ring analyses to quantify responses and recovery after droughts [54]; and tree-ring analyses of dead trees to infer mortality mechanisms [55].

4. Develop wood traits that reflect function and process.

Parameterization of functional plant types in next-generation models requires wood trait data that are directly and functionally linked to simulated processes. For instance, simulating hydraulic failure of trees requires information on loss of hydraulic conductivity, which can be obtained from xylem vulnerability curves. Another relevant trait is nonstructural carbon storage in wood [56], which relates to reserve status, osmotic regulation, drought responses [47,57,58], and next-year growth [59,60]. Some of these functional traits have already been used in recent studies to improve model performance in dry forests [11]. Wood density, a commonly used trait in vegetation models [15,61], is functional in terms of life history of tree species through its association with ecological guilds and species-specific demography [62]. Yet, from the viewpoint of functional wood biology, wood density is arguably best considered an emergent property. The rather poor associations of wood density with tree hydraulics [58] and mortality [63] seem to support this.

5. Understand dynamic allocation of biomass in trees.

Several next-generation models simulate biomass allocation dynamically, allowing functional tree responses to climatic variation and resource competition. Yet, biomass allocation to tree organs is poorly quantified empirically and dynamic allocation formulations are rather primitive. When combined with studies on leaves, roots, and reproductive structures, wood biology can help inform the pathways of biomass increment to tree organs. Specific contributions of wood biology include understanding turnover of sapwood to heartwood, relating **nonstructural carbohydrate** levels to organ growth, lag effects in cell production and division [20], and temporal shifts in allocation to different wood organs. Important insights can be obtained from xylogenesis monitoring, studies relating temporal variation in reproductive output, wood production, and root growth [64], and comparisons of tree-ring chronologies with tree-growth simulations [65]. The study of nonstructural carbohydrates is of particular importance as this

carbon pool has been shown to mitigate climate impacts [66], nutrient limitations [67], and reduce mortality rates [68].

6. Quantify nutrient cycling and effects of nutrient limitation.

A large share of forest nutrients is stored in wood, mostly in tree stems [69]. These are highly complex and dynamic pools, due to strong differences in concentration across tissues (cambium, xylem, phloem), mobilization in sapwood, and formation of heartwood. Very little is known about nutrient cycling in living wood, nutrient release during decomposition, or how nutrient availability limits tree functioning and growth. Wood biology can assist in quantifying nutrient stocks and dynamics, both in alive and dead wood [70].

Implementing the Agenda: Strategy and Challenges

How can the proposed agenda be implemented? We propose a multipronged strategy that is also cognizant of several challenges.

1. Standardization of wood biological measurements and analyses.

Many of the wood biological methods shown in Figure 2 have a short application history, resulting in unstandardized procedures and measurements. For instance, different types of dendrometers exist (band or point dendrometers), that measure variations in tree diameter or circumference at different temporal resolution and with (partial) or without bark removal. Considerable methodological variation also exists in the collection and analyses of micro core data in xylogenesis studies, and in the frequency, measured compounds, and measurement accuracy of nonstructural carbon [57,71]. This methodological variation likely induces errors and potentially structural biases in measurements and hampers comparative meta-analyses. Guiding protocols for measurements are needed [72] and inspiring examples exist for functional traits [73]. Standardization is also needed for data analysis [74,75] and interpretation of dendrometer data [76,77].

2. Data storage and availability.

Availability of, and access to, data highlighted in Figure 2 varies widely. For instance, xylem vulnerability curves, wood density, and ring-width chronologies are available in open-access databases (TRY [78], ITRDB [79]). However, information on wood phenology, wood residence time, and sap flow is poorly accessible. For all data types, poor documentation of sampling protocols and metadata cause uncertainties in data representativity and generalizability. Increasing data availability and access will importantly support model development [15] and stimulate data-model integration.

3. Target specific regions and forest types.

Development and testing of next-generation models is best concentrated on forest sites representative of major ecoregions, forest types sensitive to climate change [80], and locations where (long-term) empirical studies can be conducted. These first two criteria have not received much attention because data-model integration has mainly been conducted at sites with ample data availability. Past research foci on temperate, Mediterranean, and boreal forests in Europe and North America, has left important data gaps for (wet and dry) tropical forests [81], woodlands, and many Southern Hemisphere and montane forests.

4. Data-model integration by design.

Numerous scientists, both empiricists and modellers, have called for data-model integration (model-experiment integration, ModEx). Data-model comparisons are much needed and there are many examples of valuable benchmarking studies using wood scientific data [21,22,66,82], ecosystem experiments [25,30], or other empirical data [83]. In most of these examples, benchmarking is achieved by running models for locations of empirical studies or experiments. We argue that data-model comparisons will be more effective when empirical and modelling studies are integrated 'by design' (cf. [31]), that is, based on a common research setup and conducted in parallel. So far, this is rarely the case, but valuable examples exist [11]. Much interdisciplinary dialogue is required to maximize comparability between model parameters and empirical data.

Concluding Remarks

The development of 'big-leaf' vegetation models benefited from ground-breaking theoretical and empirical research on leaf physiology and the increased availability of Earth observation data. In a similar fashion, the development of next-generation models could greatly benefit from improved theoretical and empirical understanding of tree water transport and limitation, tissue growth, dynamic biomass allocation, and the roles of source versus sink limitation in tree growth. We have argued that wood biology can provide an important contribution by delivering insights into these processes and providing data for model benchmarking. This contribution can be realized if research focuses on key knowledge gaps, addresses key questions (see Outstanding Questions), and tackles several methodological challenges. We stress that achieving this requires intensive collaboration between wood biologists, model developers, and model users.

Outstanding Questions

How are cellular growth processes in wood determined by seasonal climatic fluctuations, carry-over effects of previous years, genetic factors, hormonal regulation, and dynamic biomass allocation?

Can the growth of tree stems (and their wood density, vessel characteristics) be simulated in process models of wood cell development?

To what extent, and in which situations, is tree biomass growth limited by carbon supply (source limitation) or by conditions allowing tissue growth (sink limitation)?

How do drivers of tree growth vary across forest types and to what extent are they modified by environmental change?

Why do trees die and what is the role of photosynthesis, water availability, hydraulic failure, and availability of non-structural carbohydrates in determining mortality risk?

How does competition for light, water, and nutrients among trees shift under climate change (drought, warming, CO_2 enrichment)?

To what extent do trees respond by acclimation and adaptation to climate change? How can adaptation be included in vegetation models?

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